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ORIGINAL ARTICLE

Microphytoplankton in a tropical oligotrophic estuarine system: spatial variations and tidal cycles

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Abstract
Camamu Bay is a shallow estuarine system, and its circulation pattern is governed by tidal forcing. The system is formed by four sectors including the main channel and three hydrodynamic regions, delimited by the influence of the five tributaries. Water samples were collected in two different pluviometric periods (dry and rainy), at nine sampling points over the three hydrodynamic regions, and at a mooring (13°52′27.42″S, 38°57′46.19″W), in the main channel, where samples were collected every 3 h over cycles of spring tides. At each sampling station, physicochemical variables were measured and water samples were collected for analysis of dissolved inorganic nutrients and chlorophyll a, composition and cell density studies of microphytoplankton. A total of 201 taxa were identified, and the great majority of the taxa were from the marine environment. The taxonomic composition varied between the hydrodynamic regions, with greater chain-forming diatom richness, in the two study periods. Although the highest concentration of dissolved inorganic nutrients was observed in the rainy period, microphytoplankton cell density did not increase in this period. The patterns of the estuarine phytoplankton community in tropical oligotrophic systems are still little known when compared to the temperate regions. Camamu Bay is one of the last known areas in the tropical South Atlantic, and this study confirms its oligotrophic characteristics, based on abiotic and biotic conditions. We highlighted the importance of knowledge of pristine coastal systems as a tool for the evaluation of anthropogenic changes in these areas.

Keywords Camamu Bay · Marine microalgae · South Atlantic · Spring tides

1 Introduction

The phytoplankton is a highly diverse polyphyletic group, formed by photosynthesizing microalgae and cyanobacteria, (Margalef 1978; Reynolds 2006) and accounts for about half the primary productivity of the Earth (Cloern and Dufford 2005; Falkowski and Raven 2007; Tilstone et al. 2017). Between 4000 and 5000 marine species are recognized (Sournia et al. 1991; Vaulot 2001; Granéli and Turner 2006; Vargas et al. 2015), although there is a general consensus that this number is underestimated for the true phytoplankton diversity (Vaulot 2001).

The phytoplankton organisms colonize the upper part of the water column, up to the limit of light penetration (Vaulot 2001). The taxonomic composition, population abundance and community structure and their distribution patterns are strongly influenced by physical processes (e.g., currents and turbulence) and chemical variations (e.g., nutrient influx) of the water (Ghosal et al. 2000; Rabalais 2002), in addition to the between-species interactions (e.g., competition for resources and grazing pressure) (Margalef 1978; Litchman and Klausmeier 2008). Primary productivity in aquatic systems thus responds to the action of bottom-up (e.g., light and nutrient availability) and top-down factors (e.g., herbivores) that control the phytoplankton biomass, composition and diversity (Metaxas and Scheibling 1996).

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The phytoplankton is the most important group of primary marine producers and makes important contributions, especially in coastal environments such as estuaries (Boney 1975). In function of the terrestrial influx and organic discharges of anthropogenic origin, these environments have high support capacity for the phytoplankton community. This permits the maintenance of high primary productivity rates (Kjerfve 1990; Attrill and Rundle 2002; Cloern et al. 2014) and consequently of other important ecosystemic services, because it represents the first transference link of primary energy in the aquatic food chains sustaining the biomass of the upper trophic levels (Cloern and Dufford 2005).

Estuaries are environments with particular characteristics determined by the entry of river water and a strong addition of mechanical energy, the tides (Simpson et al. 1990; Cloern 1991). Due to pulses of nutrients into the water column (e.g., nutrient re-suspension to more illuminated regions), the tides can cause temporal variations in the phytoplankton community composition, structure and distribution, especially in shallow coastal waters, where generally this fluctuation periodicity is more notable (Blauw et al. 2012). The patterns of the estuarine phytoplankton community, especially in tropical oligotrophic systems, are still little known when compared to the extensive number of studies carried out on estuarine systems in temperate regions (Rochelle-Newall et al. 2011; Manna et al. 2012; Pan et al. 2016).

Camamu Bay is a shallow estuarine system, with a circulation pattern governed mainly by tidal forcing (Amorim et al. 2011), with a predominance of marine influence, most notably in periods with less rainfall when the fluvial inputs are even less pronounced (Amorim et al. 2015). Surrounded by small towns, the bay is inserted in a hydrographic basin which presents one of the best states of conservation on the Brazilian coast (Hatje et al. 2008), where effects from anthropogenic pressure that are commonly reported in other tropical estuaries have not yet been observed (e.g., Figueiredo et al. 2007; Veronez Júnior et al. 2009; Thrush et al. 2013; Van Chu et al. 2014).

Camamu Bay is a system formed by four sectors including the main channel, from the entrance of the Bay with direct communication with the adjacent coastal area, and three ramifications, delimited by the influxes of the five tributaries that flow in from the north, south and central sector (Menezes 2011; Amorim et al. 2015). Considering this hydrodynamic configuration, and starting from the hypothesis that the microphytoplankton structure and composition vary between the regions of the bay and over the tidal cycles, the objectives of the present study were to (1) characterize the microphytoplankton community composition and structure and (2) quantify the relative importance of the environmental variables for the community patterns, related to the hydrodynamic characteristics and rainfall. Although it is the third largest bay in Brazil (Souza-Lima et al. 2003), it is still one of the least-known regions of the coast (Leão et al. 2003), and because it is a pristine tropical estuarine system (Carreira et al. 2016), it can serve as a model for studies of potential environmental changes, and therefore, it is important to know about its natural characteristics.

2 Materials and methods

Study area – Camamu Bay (Fig. 1) is situated on the central coast of the state of Bahia, Brazil (13°40.2′S to 14°12.6′S and 38°55.8′W to 39°9.6′W), a region with a hot and wet climate, 25 °C mean annual temperature, high rainfall, between the isoietas 2400 and 2600 mm year^{-1} (CRA 2007).

The hydrodynamic circulation inside the bay is forced by tides, with a maximum range of 2.7 m during the high tides and speeds that range from 0.6 to 1.2 m s^{-1} (Amorim et al. 2015). The main river components that make the bay an estuarine system are: Sirinhaém River is located in the northern part, a shallow channel with 7.3 m average depth. The rivers Igrapiúna, Pinaré and Sorojó are in the central part, a shallow zone, with 3.0 m average depth and maximum depth of 7.0 m, inside the river channels, and the Maraú River is located in the southern part, with 6.2 m average depth (Oliveira et al. 2002; Hatje et al. 2008; Amorim et al. 2011). The Maraú channel is a partially mixed system, the Sirinhaém channel is well mixed during the spring tides and partially mixed during the neap tides, and they are very mixed from the bay entrance to the central region. The system has a seasonally controlled cleaning/purifying capacity, and the water is renewed every 90 days in the dry periods and every 30 days in the rainfall periods (Amorim et al. 2015).

Sampling design – Sampling was conducted during spring tides, under two different pluviometric periods. The first was in October 2014, after an accumulated rainfall of 198.2 mm (rainfall period), and the second was in January 2015 after a total rainfall of 93.2 mm (dry period), considering the 30-day period prior to each sampling.

The spatial samplings were made at nine sites, distributed three by three (Fig. 1), in each one of the hydrodynamic regions (Serinhaém, Central and Maraú) of the Camamu Bay. Time-series sampling were made at a mooring (13°52′27.42″S 38°57′46.19″W), at 3-h intervals, covering a total variation of 12 h over two tidal cycles (spring tides), in October 2014 and January 2015. The mooring, at the bay entrance (Fig. 1), was chosen because

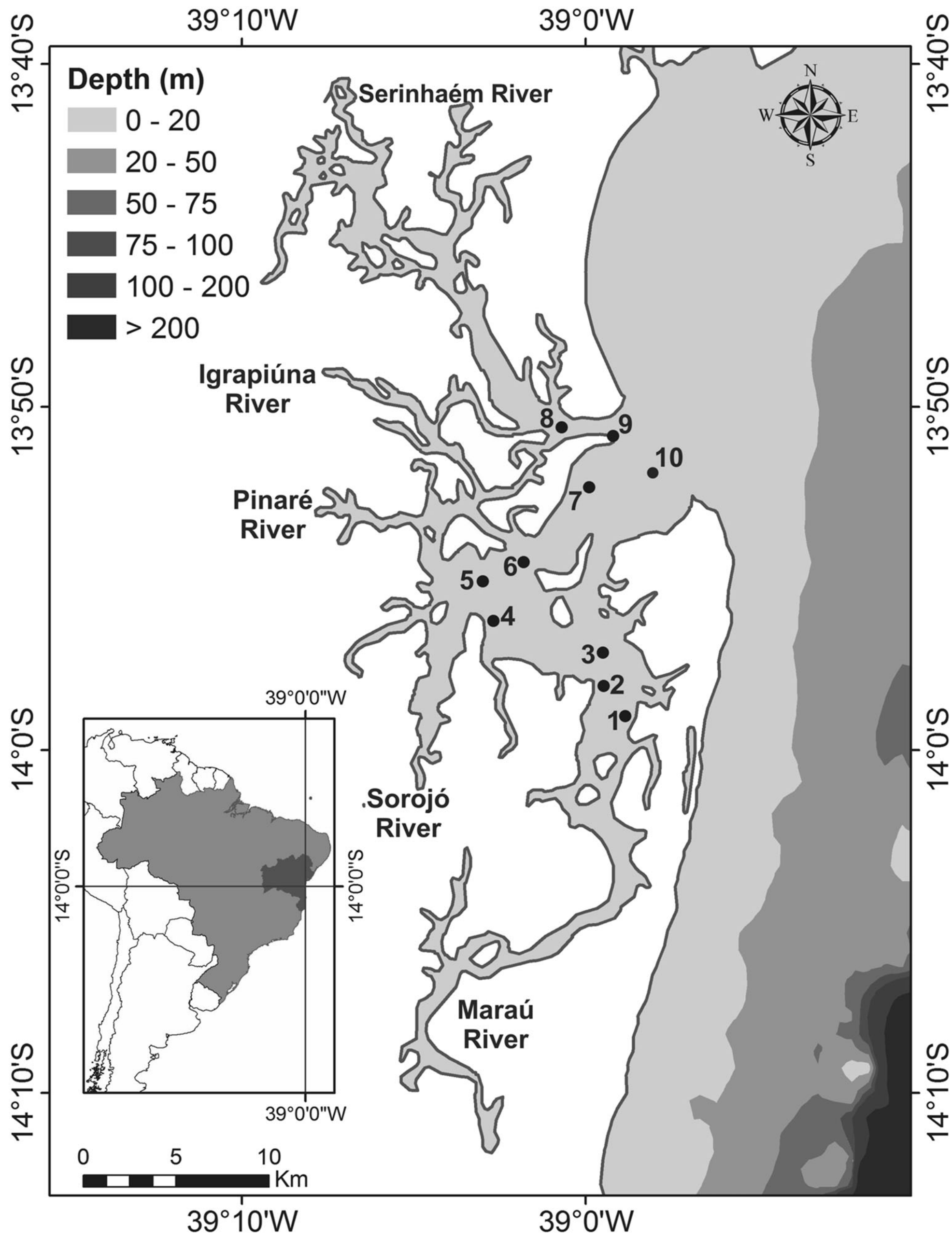


Fig. 1 Camamu Bay map with a location of sampling stations in the Maraú (points 1–3), Central (points 4–6), Serinhaém (points 7–9) and in the mooring (point 10)

it is representative of all the water exchange of the system, following hydrodynamic modeling of the area, according to Menezes (2011).

Environmental sampling – The rainfall data were obtained from the National Meteorological Institute (INMET 2001) from records of the automatic meteorological station (13°54′S, 38°58′W) in the municipality of Maraú—Bahia. The fluvial discharges of the main tributaries were calculated using the equation by Smith et al. (1999).

At each sampling station and at each hour of the tidal cycle, the temperature, salinity, pH and water dissolved oxygen were measured in situ using a multiparameter meter (Hanna HI 9829, São Paulo, Brazil). Water transparence was estimated by Secchi disk disappearance depth measurements.

Water samples (5 L) were collected (42 samples/period), using a Van Dorn bottle, for nutrient and chlorophyll *a* analyses. The samples were stored in polyethylene flasks, previously washed with HCl and distilled water, and samples were immediately filtered after each collection using a vacuum pump with fiberglass filters (Whatman GF/F—0.7 µm pore, Sigma-Aldrich, Missouri, USA) until they were clogged. Aliquots of 250 mL of the filtrated volume of each sample and the filters, wrapped in aluminum paper, were kept frozen for, at most, two weeks until the respective analyses were made.

The dissolved inorganic nutrients (nitrite, nitrate, ammonium, phosphate and silicate) were analyzed by the spectrophotometric method according to Grasshoff et al. (1983). To analyze the chlorophyll *a*, the trichromatic method was performed in acetone extracts and the concentrations were calculated according to Jeffrey and Humphrey (1975).

Microphytoplankton sampling – At each sampling station and at each hour of the tidal cycles (time-series sampling), 250 mL water samples (14 samples/period) were collected by a horizontal tows using a plankton net (20 µm mesh opening) to study the microphytoplankton community composition, and 1 L water samples (42 samples/period) were collected from the subsurface ($\sim$ half a meter deep) with Van Dorn bottle, for quantitative analyses. All samples were stored in dark polyethylene flasks and fixed with 1% lugol.

The qualitative analyses were carried out by observations on slides, under a light microscope (Olympus CX31, Tokyo, Japan). The taxa were identified using the following references: Cupp 1943; Cleve-Euler 1955; Wood 1968; Dodge 1985; Balech 1988; Hernández-Becerril 1996; Tomas 1997; Tiffany and Hernández-Becerril 2005; Tenenbaum 2006; Throndsen et al. 2007.

Quantitative analyses to determine microphytoplankton cell densities (cell L^{-1}) were made according to the Utermöhl (1958), using 50- or 100-mL sedimentation chambers, depending on the sample, with counting of the bottom of the chamber using an inverted microscope (Motic AE 2000, Hong Kong, China) at 200× to 400× magnification.

Statistical analyses – The environmental variables were analyzed with the Kruskal–Wallis analysis of variance, after checking the assumptions for parametric analyses (normality and homoscedasticity) using the Shapiro–Wilk and Levene test followed by the value multiple comparison test to assess the occurrence of significant differences ($P < 0.05$) in the physiochemical variables, dissolved inorganic nutrients and chlorophyll *a* (1) between the hydrodynamic regions of the bay and (2) between the tidal cycles.

The microphytoplankton community of Camamu Bay was characterized from measurements of species richness (S), the Shannon diversity index (H′) and the Pielou species evenness (J′).

To observe the ranking of the samples as functions of the dissimilarity in species composition and abundance (1) between the hydrodynamic regions of the bay and (2) over the tidal cycles, non-metric multidimensional scaling (NMDS) was carried out based on distance matrixes, calculated from the Bray–Curtis index. The occurrence of significant differences in community composition (1) between the hydrodynamic regions of the bay and (2) the times of the tidal cycle, in the two sampling periods, was tested by permutational multivariate analysis of variance (PERMANOVA, 999 randomizations, $P < 0.05$) based on the Bray–Curtis dissimilarity index.

Analyses of variance of the microphytoplankton density were made using *two-way* ANOVA, verifying the prerequisites for parametric analysis (normality and homoscedasticity), with the Shapiro–Wilk and Levene tests, respectively, and the value multiple comparison test *P* ($P < 0.05$) a posteriori to assess the occurrence of significant differences (1) between the hydrodynamic regions of the bay and (2) during the tidal cycles.

To quantify the relative contributions of the environmental variables in explaining the patterns of species composition and cell density in function (1) of the spatial distribution in the bay and (2) over the tidal cycles, a variation partitioning analysis was performed (Borcard et al. 1992; Peres-Neto et al. 2006), using the analyzed environmental data, separated into four groups: (1) tide height; (2) riverine discharges; (3) dissolved nutrients (i.e., nitrite, nitrate, phosphate, silicate); and (4) physicochemical (i.e., temperature, salinity, transparency, pH and dissolved oxygen). The environmental data were standardized because of their different measurement units, and the Hellinger transformation was used for the cell density data (Legendre and Gallagher 2001). All the statistical analyses were carried out in an R environment (R Core Team 2016).

3 Results

Environmental variables – The fluvial discharges ranged from 0.70 to 5.56 $m^3\ s^{-1}$ during the two sampling periods, higher in the rainy season (Table 1). The Camamu Bay estuarine system was characterized by mean transparency values in the water column of 1.3 ($\pm$ 0.6) m to 2 ($\pm$ 1) m, water temperature ranging from 26 ($\pm$ 0.2) °C to 30 ($\pm$ 0.5) °C and salinity of 32 ($\pm$ 1.6) in the two periods. The mean pH values of the water were 8.2 ($\pm$ 0.1) in the two periods. The water physicochemical variables did not vary significantly between the hydrodynamic regions, nor at the mooring, in tidal cycles.

Dissolved oxygen and temperature were the only variables that presented significant differences between the sampling periods. Dissolved oxygen saturation rates were above 100% in the first (rainy) sampling period (106.6 $\pm$ 31%) and below 50% (42 $\pm$ 3%) in the second (dry) sampling period, significantly higher ($P = 0.004$) in

Table 1 Environmental variables (dissolved oxygen percentage (DO %), pH, temperature (°C), salinity, water transparency (m), concentration of dissolved inorganic nutrients (μM L^{-1}), chlorophyll *a* concentration (μg L^{-1}) and fluvial discharges (m^3 s^{-1}) in the I—first (rainy) sampling period (October 2014) and II—second (dry) sampling period (January 2015) in the three hydrodynamic regions of Camamu Bay: Serinhaém (SER), Central (CEN) and Maraú (MAR) and mooring (tidal cycles—TC) *mean (± standard deviation)

Sampling	I				II			
Region	SER	CEN	MAR	TC	SER	CEN	MAR	TC
DO (%)	117.73 (± 9.48)	128.5 (± 8.96)	121.07 (± 6.73)	107.04 (± 5.37)	43.07 (± 0.68)	46.21 (± 1.07)	47.00 (± 0.50)	40.48 (± 1.18)
pH	8.13 (± 0.11)	8.16 (± 0.01)	8.15 (± 0.02)	8.17 (± 0.15)	8.18 (± 0.38)	8.27 (± 0.16)	8.29 (± 0.05)	8.10 (± 0.16)
Temperature (°C)	25.88 (± 0.10)	25.85 (± 0.04)	26.03 (± 0.12)	25.81 (± 0.30)	29.87 (± 0.07)	30.00 (± 0.18)	30.05 (± 0.24)	29.13 (± 0.42)
Salinity	30.07 (± 1.18)	31.27 (± 0.91)	30.97 (± 0.64)	32.26 (± 4.50)	30.94 (± 0.55)	30.65 (± 0.50)	30.77 (± 0.79)	32.71 (± 1.64)
Transparency (m)	1.33 (± 0.31)	1.60 (± 0.44)	1.53 (± 0.15)	1.14 (± 0.68)	2.17 (± 0.29)	1.47 (± 0.21)	2.20 (± 0.62)	2.52 (± 1.31)
Nitrite (μM L^{-1})	0.56 (± 0.02)	0.57 (± 0.02)	0.56 (± 0.01)	0.56 (± 0.01)	0.51 (± 0.00)	0.52 (± 0.00)	0.52 (± 0.00)	0.52 (± 0.01)
Nitrate (μM L^{-1})	1.04 (± 0.09)	1.04 (± 0.10)	1.07 (± 0.03)	1.19 (± 0.11)	0.79 (± 0.09)	0.79 (± 0.12)	0.85 (± 0.09)	0.86 (± 0.07)
Silicate (μM L^{-1})	3.59 (± 0.45)	3.51 (± 0.50)	3.79 (± 0.21)	2.29 (± 0.61)	2.19 (± 0.35)	2.42 (± 0.51)	1.60 (± 0.24)	1.27 (± 0.41)
Phosphate (μM L^{-1})	0.46 (± 0.06)	0.41 (± 0.03)	0.46 (± 0.03)	0.43 (± 0.03)	0.40 (± 0.00)	0.44 (± 0.03)	0.41 (± 0.00)	0.41 (± 0.01)
Chlorophyll *a* (μg L^{-1})	3.00 (± 0.67)	2.52 (± 0.71)	2.16 (± 0.04)	2.69 (± 0.57)	0.64 (± 0.42)	0.56 (± 0.31)	1.13 (± 0.74)	0.47 (± 0.21)
Fluvial discharges (m^3 s^{-1})	3.72	5.56	4.19	–	0.70	1.05	0.79	–

the rainy sampling period. The temperature showed significantly higher values in the second (dry) sampling period ($P = 0.0003$).

Ammonium concentrations were lower than the detection level of the method (< 0.01 μM) throughout the study, and there were low concentrations, both of the other nitrogen forms (nitrite and nitrate) and also of phosphate and silicate (Table 1). The dissolved inorganic nutrient concentrations did not differ significantly between the hydrodynamic regions, nor at the mooring, in tidal cycles. But nitrite ($P = 0.0002$), nitrate ($P = 0.0003$) and silicate ($P = 0.0003$) exhibited significantly larger concentrations in the first (rainy) sampling period, as did chlorophyll *a* ($P = 0.0004$).

Microphytoplankton – A total of 201 taxa were identified during the study (Table S1). Diatoms (ca. 70%) and dinoflagellates (ca. 25%) were the most abundant groups in the specific composition and marine species predominated. Only 15 taxa identified (ca. 7%) are of freshwater habitat.

The species diversity index in the bay was always around 3 bits ind^{-1}, and there was no dominance of any taxon ($J' = 0.7$ a 0.8) under the conditions of the study (Fig. 2a, b)

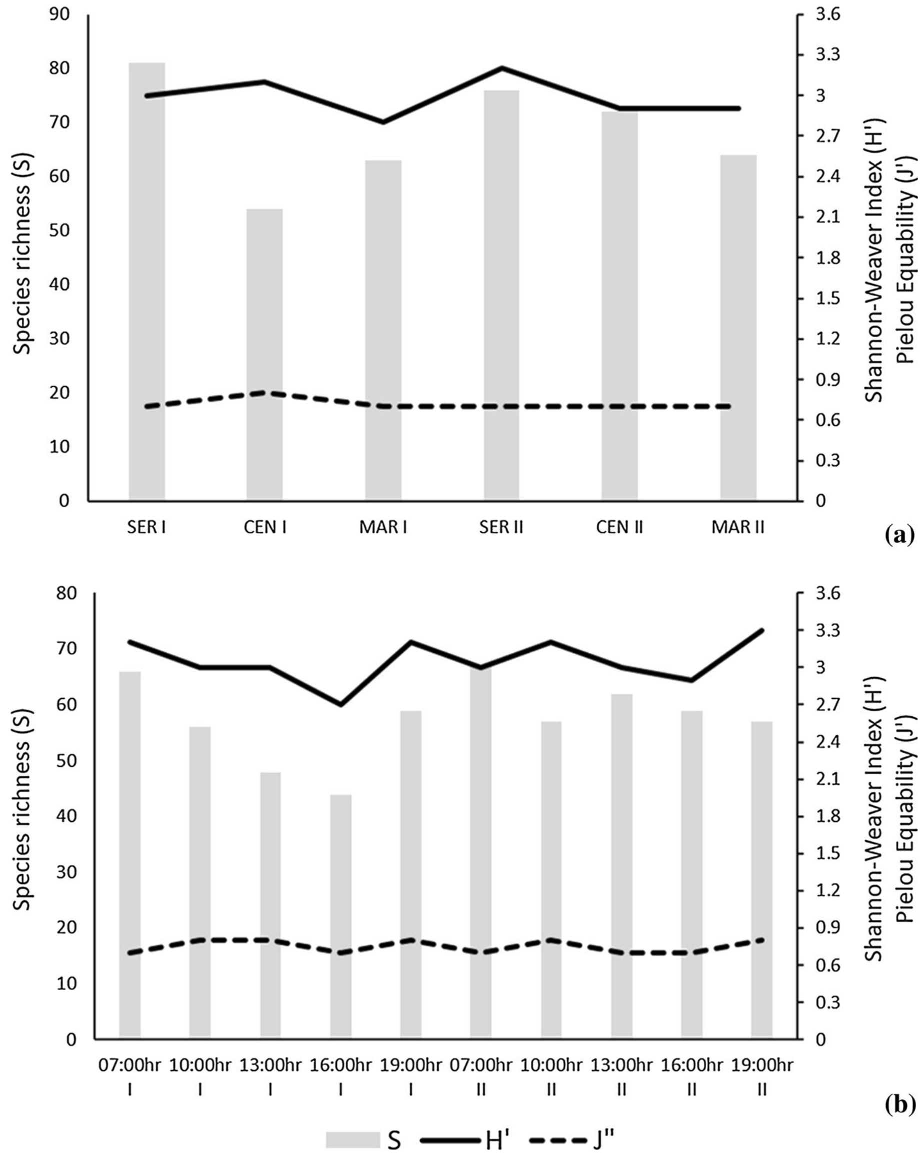
Organisms with tycoplanktonic habit represented about 13% of the taxa, and benthic species were also identified: *Ostreopsis* cf. *ovata* J. Schmidt, *Prorocentrum* cf. *emarginatum* Y. Fukuyo, *Prorocentrum* cf. *rhathymum* A.R. Loebl. et al. and *Lyngbya majuscula* Harvey ex Gomont.

Chain-forming diatoms, including *Bacillaria paxillifera* (Müller) Hendey, *Paralia sulcata* (Ehrenberg) Cleve and *Odontella aurita* (Lyngbye) C. Agardh, were the most abundant taxa in the community.

The mean cell density in the bay, considering the three hydrodynamic regions and the mooring, was 1.0×10^4 ($\pm 3.8 \times 10^3$) cells L^{-1} in the first (rainy) sampling and 1.3×10^4 ($\pm 3.8 \times 10^3$) cells L^{-1} in the second (dry) sampling period, and there were no significant differences between these periods ($P = 0.5$).

Spatial variations – A total of 144 taxa were identified in the northern part of the bay (Serinhaém—Ser), with 16 taxa occurring exclusively in this region, while 139 taxa were identified in both the central (Cen) and southern

Fig. 2 Variation the species richness (S), Shannon–Weaver Index (H′) and Pielou equability (J′) **a** in the three hydrodynamic regions of Camamu Bay: SER (Serinhaém), CEN (Central) and MAR (Maraú), and **b** in the mooring (tidal cycles) in the first (I—October 2014) and second (dry) sampling period (II—January 2015)



(Maraú—Mar) portions; the central region had 12, and Maraú had 13 exclusive taxa (Table S1).

Based on the abundance of the identified taxa, the pattern observed in the NMDS (stress = 0.16), indicated an ordination of the samples as a function of the significant differences of the composition (PERMANOVA $r^2 = 0.27$, $P = 0.001$) between the hydrodynamic regions of the bay and the significant species substitution (PERMANOVA $r^2 = 0.71$, $P = 0.001$) in each region between the two sampling periods (Fig. 3a).

The larger richness and taxonomic diversities were recorded in the Serinhaém region (Fig. 2a) in both the sampling periods. The most abundant species in this region were *Paralia sulcata* and *Bacillaria paxillifera* in the first (rainy) sampling period and *P. sulcata* and *Guinardia striata* (Stolterfoth) Hasle in the second (dry) sampling period. In the central region, the lowest species richness in the study was recorded in the first sampling period (Fig. 2a), with larger abundances of the species *B. paxillifera* and *Odontella aurita*, while in the second sampling period *B. paxillifera* and *Navicula* sp. were the most abundant species in the region. The Maraú region exhibited the lowest variation in species richness and diversity between the sampling periods (Fig. 2a), with the species *O. aurita* and *Rhabdonema adriaticum* Kützing occurring in larger abundances in the first sampling period, and *O. aurita* and *Navicula* sp. in the second sampling period.

The microphytoplankton cell density (Table 2) between the hydrodynamic regions ranged from 3.2×10^3 cells L^{-1} in Maraú (rainfall period) to 2×10^4 cells L^{-1} in Serinhaém (dry period) and did not differ significantly between the three regions ($P = 0.19$), or between the sampling periods ($P = 0.58$).

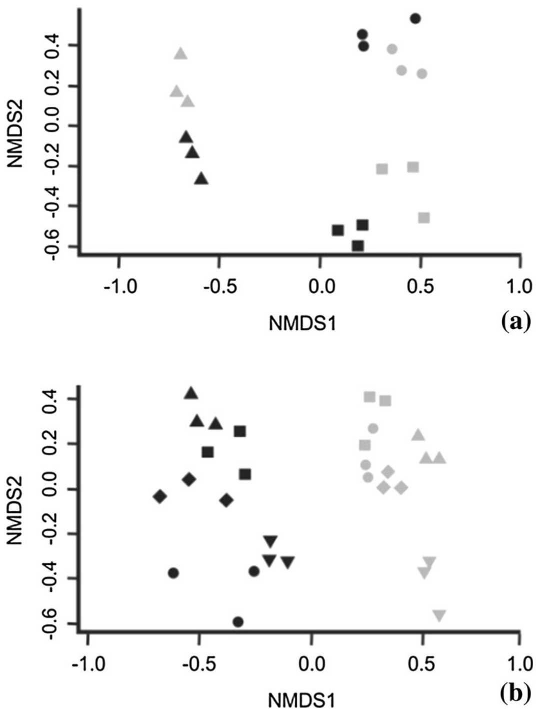


Fig. 3 Non-metric multidimensional scaling (NMDS) analysis of the taxa abundance **a** in the three hydrodynamic regions of Camamu Bay. Up pointing triangle = Serinhaém, circle = Central and rectangle = Maraú, and **b** in the mooring (tidal cycles). Down pointing triangle = 7:00 a.m., Circle = 10:00 a.m., square = 1:00 p.m., diamond = 4:00 p.m., up pointing triangle = 7:00 p.m. Black symbols = first (rainy) sampling period (October 2014); gray symbols = second (dry) sampling period (January 2015)

The variance partition indicated that the environmental variables explained about 76% of the specific composition of the microphytoplankton community. The isolated tidal variation fraction explained 19% of the variation, followed by the isolated fractions of the nutrient and physicochemical variables that each explained 14% (Fig. 4a).

For cell density, the variance partition explained 83% of the total variance, represented mainly by the nutrients fraction (41%), followed by the water physicochemical factors fraction that explained 16% (Fig. 4b).

Tidal cycles variations – A total of 118 taxa were identified at the mooring (Table 2). Considering their abundance during the tidal cycles, the samples could be ranked as a function of the differences in the specific composition between the two cycles (Fig. 3b). The pattern observed in the NMDS ranking (stress = 0.15) was supported by the significant difference between the two sampling periods (PERMANOVA $r^2 = 0.42$, $P = 0.001$), and there were no significant differences in composition between the periods of the same tidal cycle (PERMANOVA $r^2 = 0.10$, $P = 0.078$).

Paralia sulcata and *Thalassionema nitzschioides* (Grunow) Mereschkowsky were the most abundant species during the tidal cycle in the rainy period, between 07:00 h and 16:00 h, and in terms of greater abundance, *P. sulcata* was replaced by *Melosira moniliformes* (O.F. Müller) C. Agardh at 19:00 h. *Chaetoceros decipiens* Cleve and *Pseudo-nitzschia* sp. were the most abundant species during the tidal cycle in the dry period, between 07:00 h and 16:00 h, while at 19:00 h *P. sulcata* was the most abundant species.

Species richness varied more in the rainy period tidal cycle (44–66) than in the dry period (57–67). The species diversity ranged from 2.68 to 3.18 bits ind^{-1} in the rainy period tidal cycle and from 2.85 to 3.28 bits ind^{-1} in the dry period, but no taxon dominated (J′) in any tidal cycle (Fig. 2b).

The microphytoplankton cell density variation over the tidal cycles was from 6.0×10^3 to 1.2×10^4 cells L^{-1} in the rainy period and 8.3×10^3 to 2.0×10^4 cells L^{-1} (Table 3) in the dry period, but they were not significantly different ($P = 0.3$) each other. During the rainy period tidal cycle, at 13:00 h, the microphytoplankton density was significantly lower ($P < 0.001$) than at the other times of the cycle. During the dry period tidal cycle, the microphytoplankton density varied more, differing significantly ($P < 0.001$) between all the sampling times, except between 10:00 h and 13:00 h.

The variance partition showed that the variation in species composition during the tidal cycles was explained by environmental conditions at 78%, mainly by the isolated fraction of the physical–chemical variables (37%), followed by the shared fractions of the physical–chemical variables and nutrients, that explained 30% (Fig. 5a).

For the microphytoplankton density variation in the tidal cycles, the variance partition exhibited a total explanation

Table 2 Microphytoplankton cell density variation (cell L^{-1}) minimum–maximum (mean ± standard deviation) in the I—first (rainy) sampling period (October 2014) and II—second (dry) sampling period (January 2015), in the three hydrodynamic regions of Camamu Bay: Serinhaém (SER), Central (CEN) and Maraú (MAR)

	I	II
SER	1.1×10^4 a 2×10^4 ($1.5 \times 10^4 \pm 4 \times 10^3$)	6.7×10^3 a 2.0×10^4 ($1.2 \times 10^4 \pm 6.80 \times 10^3$)
CEN	4.5×10^3 a 1.1×10^4 ($7.6 \times 10^3 \pm 3.4 \times 10^3$)	9.0×10^3 a 1.5×10^4 ($1.3 \times 10^4 \pm 3.08 \times 10^3$)
MAR	3.2×10^3 a 1.6×10^4 ($9.1 \times 10^3 \pm 6.3 \times 10^3$)	8.6×10^3 a 1.4×10^4 ($1.0 \times 10^4 \pm 2.72 \times 10^3$)

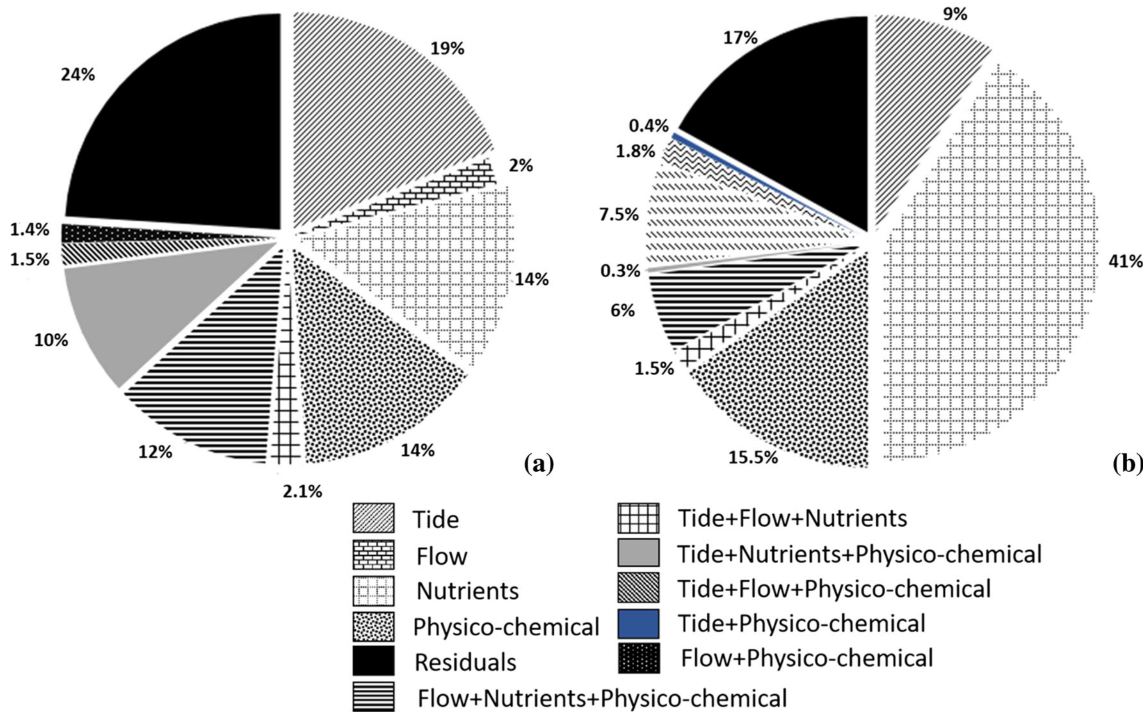


Fig. 4 Variance partition **a** of the microphytoplankton composition and **b** of the microphytoplankton cell density in the three hydrodynamic regions at the Camamu Bay

Table 3 Microphytoplankton cell density variation (cell L^{-1}) in the mooring at Camamu Bay, in tidal cycles—minimum–maximum (mean ± standard deviation) in the I—first (rainy) sampling period (October 2014) and II—second (dry) sampling period (January 2015)

	I	II
07:00 h	8.9×10^3 a 1.0×10^4 ($9.4 \times 10^3 \pm 5.6 \times 10^2$)	1.8×10^4 a 2×10^4 ($1.9 \times 10^4 \pm 3.2 \times 10^2$)
10:00 h	9.8×10^3 a 1.2×10^4 ($1.1 \times 10^4 \pm 8 \times 10^2$)	1.1×10^4 a 1.2×10^4 ($1.2 \times 10^4 \pm 6.6 \times 10^2$)
13:00 h	6×10^3 a 6.8×10^3 ($6.4 \times 10^3 \pm 4.9 \times 10^2$)	1.2×10^4 a 1.3×10^4 ($1.2 \times 10^4 \pm 4.4 \times 10^2$)
16:00 h	9.2×10^3 a 1×10^4 ($9.8 \times 10^3 \pm 6.4\times 10^2$)	1.4×10^4 a 1.5×10^4 ($1.5 \times 10^4 \pm 4.4 \times 10^2$)
19:00 h	8.3×10^3 a 8.5×10^3 ($8.5 \times 10^3 \pm 8.9 \times 10^1$)	8.6×10^3 a 8.4×10^3 ($8.3 \times 10^3 \pm 7.3 \times 10^1$)

of 84.5%, and the physiochemical variables fraction accounted for 63% of the explanation (Fig. 5b).

4 Discussion

Environmental variables – In tropical (and subtropical) environments, the rainfall is a fundamental modulator of the availability of dissolved nutrients and optical qualities of water (Bastos et al. 2005), and consequently, the larger determinant of chlorophyll *a* concentrations in the aquatic systems (Losada et al. 2003). In the Camamu Bay, region with an annual mean rainfall of approximately 1480 mm and monthly mean of 123 mm, it was observed that the water physicochemical variables were influenced by the larger riverine discharges in the rainy period (198.2 mm), causing increased in the nutrient concentrations in the system. This entry of fresh water allowed an increase in the chlorophyll *a* biomass, keeping the waters in the bay well oxygenated and saturated (> 100%) in dissolved oxygen.

In contrast, in the dry period (93.2 mm), the smaller river influxes were reflected in lower nutrient and chlorophyll *a* concentrations and the establishment of heterotrophic conditions reflected the subsaturated dissolved oxygen (~ 50%). The dissolved oxygen saturation may indicate an increase in primary productivity rates in the systems (Campelo et al. 1999), so it, in future studies, is important to include measures of primary productivity in the Camamu Bay in order to better characterize this system condition.

The increase in the nutrient concentrations during rainy periods is a condition commonly observed in a variety of

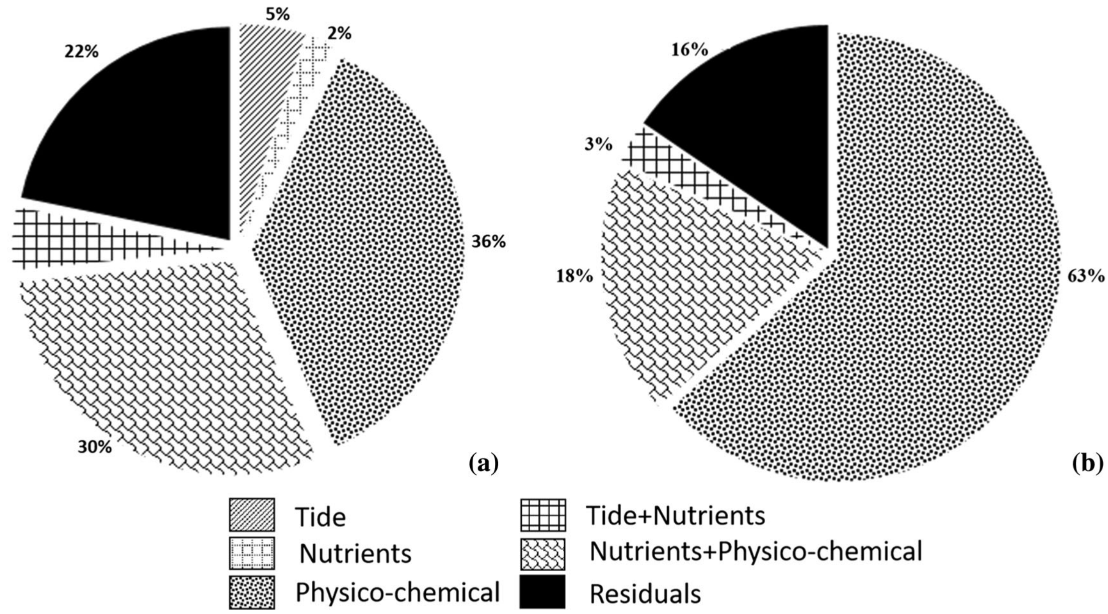


Fig. 5 Variance partition **a** of the microphytoplankton composition and **b** of the microphytoplankton cell density in the mooring (tidal cycles) at the Camamu Bay

tropical estuaries (e.g., Dittmar et al. 2001; Sarma et al. 2010; Bastos et al. 2011). However, in spite of the enrichment of the system in the period with more rain, the waters in Camamu Bay remained characteristically oligotrophic (Niencheski et al. 1999; Knoppers et al. 2002). Similar results were observed in oyster cropping areas in the bay by Affe and Santana (2016), due to small riverine discharges because of very small discharges from the tributaries that did not change significantly between the rainy and dry seasons (Amorim et al. 2011). The low anthropogenic impact was shown, for example, by the absence of influences from domestic sewage in the area (Carreira et al. 2016).

Despite the three subsystems (hydrodynamic regions) with different hydrodynamic characteristics (i.e., riverine discharges, residence time and water renewal) (Menezes 2011), significant variations were not observed in the environmental characteristics between the three hydrodynamic regions during the study periods, reflecting the great influence from the marine influx into the bay and the high mixture in the water column (Amorim et al. 2015).

Microphytoplankton – The microphytoplankton composition, during the two sampling periods, illustrated the hydrodynamic forcing in the estuarine system, and especially, the strong influence from the marine influx, shown by the species predominant in this habitat. The predominance of diatoms (i.e., larger species richness and abundance) in the bay followed a typical coastal water pattern (e.g., Garg and Bhaskar 2000; Gin et al. 2000; Procopiak et al. 2006; Silva et al. 2009; Rochelle-Newall et al. 2011; Rezende et al. 2015; Carvalho et al. 2016) as did the occurrence of tycoplanktonic species that are re-suspended by the action of turbulence in the water column (Tilstone et al. 2000; Odebrecht et al. 2002; Smayda 2002).

The diatoms comprised an important fraction (70%) of the community in the bay, as already observed in other coastal and estuarine environments (e.g., Fernandes and Brandini 2004; Lacerda et al. 2004; Silva et al. 2009). The high number of chain-forming diatoms perhaps is related to (e.g., *Paralia sulcata*, *Bacillaria paxillifera*, *Guinardia striata*, *Odontella aurita*), greater efficiency in light capture and greater nutrient storage capacity, given the higher surface/volume ratios of cells (Villareal et al. 1993; Hutchings et al. 1995; Sunda and Huntsman 1995; Klausmeier and Litchman 2001), in addition to the greater capacity to regulate fluctuation that favors their predominance in turbulent waters (Round et al. 1990).

Different depths were not compared in the present study, but the conditions of the high mixture in Camamu Bay have been reported previously by Affe and Santana (2016) due to the absence of differences in temperature and salinity in the water column. According to Amorim et al. (2015), there is partial stratification during neap tides, with differences in salinity smaller than two between the surface and the bottom, but during spring tides the water column is very mixed throughout the bay. In this region of Brazil, the semiarid climate of the interior of the state at the heads of the hydrographic regions, and the small discharges ($\sim 10\ m^3\ s^{-1}$) from the tributaries, associated with the tide intervals, result in very mixed water columns, as occurred in Todos os Santos Bay (Cirano and Lessa 2007), situated between 13°S and 22°S on the Brazilian eastern platform (Knoppers et al. 2002).

The marine influx was the main force in the microphytoplankton composition in the Camamu Bay, repeating a pattern found in tidal forced estuarine systems (Bazin et al. 2014), resulting in a high diversity of marine species in the system, during the two sampling periods. In tropical estuaries, there is alternation between periods of high rainfall, with greater riverine discharges and periods when marine influxes dominate and there is less rainfall, as these parameters most influence the species richness distribution of the phytoplankton community (Lacerda et al. 2004; Silva et al. 2009).

During the tidal cycles, the predominance of chain-forming diatoms was also observed in both the study periods. In the rainy period, *Paralia sulcata* was the most abundant species during the day (07:00–16:00 h), with an inverse pattern in the night sampling (19:00 h), when decreased that species density. The sharp reduction in salinity at night (35.5–24) possibly influenced this change, as in other systems, in which reductions in abundance of *P. sulcata* were also recorded for low-salinity conditions at the water surface (McQuoida and Nordberg 2003; Gebühr et al. 2009; Guo et al. 2014). In contrast, during the second tidal cycle (dry period) the *P. sulcata* cell density remained approximately the same throughout the day, increasing at night, when the water salinity remained high ($\sim$ 31) throughout the cycle. Because it is a tycoplanktonic species, *P. sulcata* can be considered as an example of a turbulence indicator species in the bay, and its occurrence is common in brackish and marine environments, with intense vertical mixing (McQuoida and Nordberg 2003; Gebühr et al. 2009).

The microphytoplankton community in the Camamu Bay estuarine system exhibited a similar pattern between the hydrodynamic regions. The indices of phytoplankton diversity characterize the system as of being of high diversity ($H' > 2.5$), according to the Margalef (1978) classification, and these indices were similar to those found in other coastal regions in northeastern Brazil, even the most eutrophied (e.g., Silva et al. 2009; Santiago et al. 2010). Maintaining this high diversity, considering the few resources available (i.e., dissolved nutrients) depends on processes that prevent the community from reaching competitive equilibrium, as discussed by Hutchinson (1961). Again, turbulence is indicated as a very important process, also for the phytoplankton community structure, especially in regions with relatively low nutrient concentrations (Barton et al. 2014), with turbulence facilitating nutrient re-suspension to the photic layer and maintaining phytoplankton suspension (Round et al. 1990; Ghosal et al. 2000; Barton et al. 2010; Pan et al. 2016).

Although there was enrichment of dissolved nutrients in the system in the rainy period, a corresponding increase was not observed in the microphytoplankton cell density. This result contradicts that observed in tropical estuaries that have seasonal rainfall variation, where the episodic pulses of fresh water are preponderant in the hydrodynamic and larger nutrient influx in the rainy period tends to lead to higher phytoplankton densities and biomass (Sassi et al. 1991; Eskinazi-Leça et al. 2004; Lancelot and Muylaert 2011), even in the most eutrophied (e.g., Grego et al. 2004; Honorato-da-Silva et al. 2004; Sousa et al. 2008; Costa et al. 2011; Matos et al. 2011, 2012). In Camamu Bay, the greater marine influence in the dry period and increases in the riverine discharges in the inland regions in the rainfall periods (Amorim et al. 2015) bring changes that, although they were shown in the environmental variability (i.e., differences in temperature, salinity) between the two periods analyzed did not determine significant alterations in the community structure and composition. The influence of the Brazil Current that flows all year along the Bahia coast (Signorini et al. 1989), and the predominance of marine influx in the estuarine system, may be the main factors in maintaining the oligotrophic character of the bay, even under different rainfall conditions.

Camamu Bay was shown to be a fairly mixed system in spring tides, with low nutrient concentrations even in conditions of greater riverine discharges in the rainy period. In summary, the data acquired in this study revealed the great tropical shelf water intrusions, which confers oligotrophic characteristics and marine species predominance in the three hydrodynamic regions of the system. The sampling in tidal cycles evidenced the importance of this forcing to the maintenance of the dynamic and high diversity observed in the microphytoplankton community. Microphytoplankton cell density did not vary significantly, but there were changes in species composition between the pluviometric periods, as a function of the variation of the abiotic (although discrete) conditions.

We highlighted the importance of this knowledge given the conservation conditions of the system in the face of the global climate change scenario and growing anthropogenic pressure that alters the dynamic and quality of the water in tropical estuarine systems. Camamu Bay is suggested as a potential model for studies of the ecology of the phytoplankton community, since observing community patterns in preserved oligotrophic environments serve as a basis for studies of the potential environmental changes on many systems.

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